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THE UNIVERSITY OF ALBERTA

THE ANNUAL TREE RING GROWTH OF BLACK SPRUCE IN RELATION TO CLIMATE AND DRAINAGE IN SOME NATURAL AND DRAINED PEATLANDS IN ALBERTA

BY

QING LAI DANG

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE.

DEPARTMENT OF FOREST SCIENCE

EDMONTON, ALBERTA

(FALL 1988)

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THE UNIVERSITY OF ALBERTA

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The undersigned certify that they have read, and recommended to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled The Annual Tree Ring Growth of Black Spruce in Relation to Climate and Drainage in Some Natural and Drained Peatlands in Alberta submitted by Qing Lai Dang in partial fulfillment of the requirements for the degree of Master of Science.

Victor Lieffers
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ABSTRACT

The annual tree ring growth of black spruce was studied in relation to climate and drainage in some natural and drained peatlands in Alberta. The major findings on the tree growth-climate relationship are as follows: in natural peatlands, the tree ring indices were positively correlated with the June-to-August total precipitation of the current year and at 1 and 2 year lags, but negatively related to June to August maximum temperature of the current year and at 1 and 2 year lags; the relationship between tree ring indices and minimum temperatures was linear and positive for the current year minimum temperature, but for the 1 and 2 year lags, the tree ring indices increased and then decreased with increasing temperature.

In a second project, a new procedure was developed for assessing the effects of drainage on tree ring growth. It uses both the predrainage growth of the drained site and the postdrainage growth on an adjacent undrained site as controls in estimation of the tree ring growth response following drainage. This allowed the calculation of the net response of tree ring growth on a yearly basis to peatland drainage.

Results from six peatlands which were drained 21 years previously showed: For the first 3 to 6 years following drainage, the tree ring growth did not increase

in response to drainage. After that, the amount of net increase in tree ring growth increased linearly until reaching a maximum value between 13 to 19 years after drainage. The maximum net increases ranged from 76 to 766% of the growth which the trees would have attained if the drained sites were not drained. The net increases fluctuated near the maximum value thereafter. The year to year fluctuation in tree ring index on the drained site appeared to correspond to the year to year fluctuation in the natural site.

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I. INTRODUCTION

DENDROCHRONOLOGY AND DENDROECOLOGY

Dendrochronology is the study of annual growth of tree rings (Fritts 1976). According to Fritts (1976), the science of dendrochronology was initiated by A.E. Douglass in 1904. His goal was to examine the relationship between sunspot activity and climate variation, especially precipitation variation, on the earth. He thought that the sunspot activity influenced the climate of the earth and climate affected tree ring growth, therefore sunspots might be correlated to tree ring growth. He correlated tree ring growth data to sunspot records and was able to extend the sunspot records back into the past by tree ring data (Fritts 1976). Douglass established the important procedures of dendrochronology.

At its early stage, dendrochronology was mainly used to extend climate record into the past. Later dendrochronologists, such as H.C. Fritts, extended the scope of dendrochronology and replaced some of Douglass's early quantitative methods by modern statistical procedures. As tree ring analysis has been applied to more and more disciplines, dendrochronology has been divided into many subfields, such as dendroclimatology, dendrohydrology, dendrogeomorphology, and dendroecology (Fritts 1976). Dendroecology is the application of dendrochronological techniques in ecological studies.

The principle of limiting factors states that a

biological process, such as tree growth, cannot proceed faster than is allowed by the factor most limiting to the process (Fritts 1976). According to this principle, dendroecology can be used wherever one or more environmental factors become critically limiting, persist sufficiently long, and act over a wide geographic area to cause tree ring widths or other features to vary similarly in many trees (Fritts 1976). Most applications of dendroecology, however, have been on dry land forests, especially extremely arid sites. It has rarely been used on wetland trees. Many studies (MannerKoski 1985; Lieffers and Rothwell 1987b) showed that in peatlands, water table is a critical limiting factor to tree growth. Water table is influenced by climate and other factors. This indicates that dendroecology can probably be applied to trees from peatlands.

TREE GROWTH ON NATURAL AND DRAINED PEATLANDS

Peat is an organic soil which has developed as a consequence of incomplete decomposition of wetland vegetation under high moisture and deficient oxygen conditions (Päivänen 1984). Areas with accumulated peat greater than 40cm can be defined as peatland (Zoltai and Pollett 1983). There are about 422 million hectares of peatland in the world (Kivinen and Pakarinen 1981). The total area of peatlands in Canada is nearly 118 million hectares, eleven percent of which is distributed in

Alberta; this is about twenty percent of Alberta's total land area (Tarnocai 1984; Päivänen 1985). There is a paucity of information on tree growth and production on natural peatlands. Compared with upland sites, however, the tree growth rates in natural peatlands are generally low (Payandeh 1973; Makitalo 1985). The vast area of Alberta peatlands and the success of drainage projects in Scandinavian countries suggest a great potential for wood production from Alberta peatlands.

In peatlands, water table is considered as to be an important factor both in affecting tree growth and in controlling the physical conditions of the substrate. In natural peatlands, high water table causes low substrate temperature, poor aeration and lack of oxygen in the soil, and inadequate available nutrient supply (Payandeh 1973; Makitalo 1985; Mannerkoski 1985). These factors affect rooting patterns. Trees which have taproots may have dominantly lateral roots when the water table is high (Heikurainen 1971). High water table also limits the growth of roots, the number of short roots, the average and maximum extension of the roots downward in the substrate, and the presence of mycorrhizae (Paavilainen 1966; Boggie 1972; Lieffers and Rothwell 1986 and 1987b). In wet peatlands, tree roots only grow on hummocks, while on dry sites, they can penetrate 60cm into the peat substrate (Lieffers and Rothwell 1987b).

Water table in peatlands fluctuates frequently (Dai et al. 1972; Mannerkoski 1985). In terms of the physiology of trees, the fluctuation of water tables is more important than the average depth to water table (Mannerkoski 1985). Studies by Mannerkoski (1985) demonstrated that the vertical reach of tree roots in peatland depends more on the upper limits of water table fluctuation than the average level. When water table fluctuated, tree roots were closer to the peat surface than when the water table was held at a level equal to the mean level for the fluctuating site.

High water table in peatlands also limits the above ground growth of trees. Lieffers and Rothwell (1987b) indicated that the tree size of black spruce (Picea mariana (Mill.) B.S.P.) and tamarack (Larix lariciana (Du Roi) K. Koch.) was positively correlated with the depth to water table. Boggie et al. (1976) found that the stem volume, tree height and foliage area of Pinus contorta (Loud.) Dougl. were positively related to the depth to water table.

The adverse effects of high water table and its fluctuation vary with seasons and tree age. Generally, high water table is more detrimental late in the growing season (Pelkonen 1975; Paivanen 1984). Roots of older trees must occupy a larger volume of soil for nutrient collection and anchoring the tree. The optimum depth to water table, therefore, becomes deeper as the tree become

larger (Mueller-Dombois 1964).

The temperature regimes in peatlands also affect tree growth and phenology. Low substrate temperatures in natural peatlands limit root size, rooting depth and top growth in black spruce and tamarack (Lieffers and Rothwell 1987a and 1987b). Lieffers and Rothwell (1987a) also found that because drainage increased the surface substrate temperature, bud flush of terminal leaders and both male and female cones was earlier in drained areas.

While climate affects the accumulation of the peat (Paivanen 1984) and the physical conditions of the substrate, it also directly affects tree growth and production (Fritts 1976; Josza et al. 1984). However, there is a lack of knowledge on the relationship between climate and tree growth on natural peatlands.

The tree growth on natural peatlands, however, can be considerably improved by drainage (Heikurainen and Kuusela 1962; Stanek 1968 and 1977; Boggie 1972; Boggie et al. 1976; Payandeh 1973; Richardson 1981; Wang et al. 1985; Trottier 1986). Peatland drainage for forestry purpose has been practiced extensively in Finland, France, Germany, Scandinavia and U.S.S.R. (Payandeh 1973). Some small scale peatland drainage experiments have also been conducted in Canada (Hillman 1987).

Drainage lowers water table and improves the physical conditions of the substrate and the air layer near the peat

surface. The improvement of tree growth in response to these changes are well documented. Lieffers and Rothwell (1987b) observed that the fine root biomass and the maximum rooting depth all increased after the peatland was drained. The increased root growth improves the tree's capacity for water and mineral uptake. Two to five fold increases in tree height and D.B.H. growth following peatland drainage were reported (Stanek 1968; Payandeh 1973; Richardson 1981; Wang et al. 1985). Stanek (1977) demonstrated that drainage increased the site index (tree height at 100 years of age) for black spruce by 4 to 6 metres respectively for fen-marsh and bog sites. Trottier (1986) reported that drainage increased the wood production rate by more than four folds. The total increases in tree growth which were caused by drainage, however, were not distributed evenly over the entire postdrainage period. Lieffers and Rothwell (1987a) also suggested that following drainage there might be an initial response period when trees grow slower than normal. Studies from Finland (Seppälä 1969) did not report a slowing in growth but indicated that tree growth did not increase for the first few years after drainage. The patterns of increases following drainage are still unclear.

Various methods (Heikurainen and Kuusela 1962; Heikurainen 1964; Stanek 1968 and 1977; Payandeh 1973, 1975 and 1982; Wang et al. 1985) have been used to evaluate the

drainage effects on tree growth where drainage occurred half way through the life of the trees. However, there are some problems associated with these methods. In addition, none of these methods are capable of determining the patterns of net response in tree growth following drainage. An alternative method for estimating the patterns of net response in tree growth following peatland drainage needs to be developed.

OBJECTIVES

The objectives of this study were: 1. to determine the relationship between the annual tree ring growth of peatland black spruce and precipitation and air temperature; 2. to develop a new method for evaluating the patterns of net response in tree ring growth to peatland drainage; 3. to describe the pattern of growth response of black spruce following drainage.

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II. THE ANNUAL TREE RING GROWTH OF BLACK SPRUCE IN RELATION TO PRECIPITATION AND AIR TEMPERATURE IN SOME ALBERTA PEATLANDS

INTRODUCTION

Annual rings of trees in upland areas have often been related to climate (Fritts 1976; Jozsa et al. 1984) but there is little information on the impact of yearly variation in climate on growth of trees in wetland areas. In natural peatlands, tree growth is dependent on the depth of water table (Boggie and Miller 1976; Mannerkoski 1985; Lieffers and Rothwell 1987b). Generally, root growth of peatland trees is restricted by high water table (Boggie 1972; Boggie and Miller 1976; Lieffers and Rothwell 1987b), but black spruce (Picea mariana (Mill.) B.S.P.) and tamarack (Larix laricina (Du Roi) K. Koch.) will increase rooting depth and fine root biomass when the water table is lowered (Lieffers and Rothwell 1987b). The above ground tree growth is also positively related to the depth to water table (Boggie et al. 1976; Lieffers and Rothwell 1987b).

The depth to water table in peatlands is regulated by many factors, but probably precipitation and temperature are the most important in the control of seasonal and yearly variations (Mannerkoski 1985). Increases in water table follow heavy rainfalls (Dai et al 1972; Munro 1984). If high water table depresses the growth of peatland trees, then years with much greater than average precipitation should also have reduced growth rates. Temperature regulates water table by its influence on

evapotranspiration (Mannerkoski 1985), but it also directly affects tree growth (Van Cleve et al. 1983; Tryon and Chapin 1983) and phenology (Lieffers and Rothwell 1987a). Van Zinderen Bakker (1974) observed a reduction in net carbon assimilation of black spruce at leaf temperature greater than 15^0C and low light intensities.

The objectives of this study are to examine the relationship between the annual ring growth of black spruce from natural peatlands and yearly variation in precipitation and air temperature.

MATERIALS AND METHODS

The study sites were located in a large undisturbed treed fen 11 km east-northeast of Slave Lake ($55^0$20'N; $114^0$34'W). Forests in this area consist of black spruce with scattered tamarack. Understories are dominated by Ledum groenlandicum Oeder, Rubus chamaemorus L. and Sphagnum magellanicum Brid. Two sites, 1 km apart, were selected. Fifteen dominant-codominant black spruce were cut from each site in the spring of 1987, before the initiation of diameter growth. The sample trees were approximately 87 years old. Three cross sections were taken from the bole of each tree at the tree base, and at 30 and 130 cm height. The sections were air dried and sanded by a belt sander. The ring width of all the sections were measured on a computerized tree-ring measuring device (Clyde and Titus 1987). Four radii along

the longest and the shortest diameters were measured for each section. Ring width data were plotted against tree age. Crossdating (matching tree ring-width variations among trees) was conducted to identify false and/or missing rings (Fritts 1976). Cross-dating was done by comparing graphs of tree ring width versus age, among radii within sections, then among sections within trees, among trees of the same site, and lastly between the two sites (Fig. II.1). Missing and/or false rings were confirmed by careful examination of the discs. Correction was made for missing/false rings. The tree-ring series of different radii were averaged to get the mean tree-ring series of that section. The mean-sensitivity (Ms) of each section is calculated using the following formula,

$$Ms = \frac{1}{n-1} \sum \frac{|X_{t+1} - X_t|}{(X_{t+1} + X_t)/2}$$

where: X_{t+1} and X_t are the widths of two neighboring rings; $t = 1, 2, \ldots, n-1$; and n is total number of rings.

and is interpreted that the larger Ms is, the better the tree ring data can reflect climate fluctuation (Fritts 1976). In this study, the discs at 30 cm height had the largest average mean-sensitivity value and fewer missing or false rings than the base sections. So the tree ring data from discs at 30 cm height were used for climate-tree-growth analyses. In order to remove the effects of tree

age on tree ring width, the tree ring width data were modelled by a negative exponential function each observed ring increment was divided by the corresponding value from the regression equation, to give tree ring indices (Fritts 1976). Because the climate data were available only back to 1925, only the tree ring data for the last 62 years of growth (when ring width decreased with tree age) were used. One way analysis of variance showed no significant difference among tree ring index series of different trees from the same site, therefore, they were averaged to obtain the site chronologies of each site (Fritts 1976) for further analysis. The chronologies for the two sites were highly correlated ($r = 0.82$).

The temperature and precipitation data from Slave Lake Airport were obtained from the Monthly Record (Environment Canada) for the periods of 1925-1962 and 1970-1986, respectively. Precipitation variables used for the analysis were: total precipitation of pregrowing season (previous September to current May), and growing season (June to August) of the current year and at lags of one and two years. Temperature variables used were: growing season (June to August) mean, maximum, minimum temperatures of current year, and at one and two-year lags.

Linear and quadratic polynomial regressions were used to determine the relationship between the tree ring index and each of the climate variables. The possible

intercorrelations among the climate variables were evaluated using the correlation matrix of climatic variables and principal components analysis of the correlation matrix (Dixon et al. 1985).

RESULTS

Tree ring growth and precipitation

The tree ring index was positively correlated to growing season precipitation of the current year (Fig. II.2a) and at one (Fig. II.2b) and two-year lags (Fig. II.2c) for both sites. The correlation was the strongest for the precipitation at one year lag. Most of the precipitation data were within the range of 71 to 325 mm, with exceptions of years with 410 and 424.7mm. These points appeared to be outliers and were eliminated from the regression analysis. The two data points that were eliminated were generally below the regression lines; this suggests that there was probably reduction in growth in years with very high summer precipitation and in the following two years.

There was no significant relationship between pregrowing season precipitation and tree ring index.

Tree ring growth and air temperature

For both sites, tree ring index was not correlated with average growing-season temperature (Fig. II.3), but was correlated with maximum and minimum temperatures

(Figs. II.4 and II.5; Tables II.2 and II.3). The maximum temperature of the current year and at one and two year lags were all negatively correlated with tree ring index (Fig. II.4 and Table II.2). Tree ring growth decreased linearly as maximum temperature increased. There was little variability in slopes and intercepts of regression lines between the two sites and among the current year, and one and two year lags. The maximum temperatures of the current year and at one year lag were more strongly correlated with tree ring index than that at two-years lag.

The tree ring index was positively correlated with the minimum temperature of the current year (Fig. II.5a; Table II.3). However, the regression for site 2 was not significant at the 0.05 level. The relationship between tree ring index and minimum temperature at one and two year lags were modelled by a quadratic polynomial (Table II.3). As minimum temperature at one year lag increased, tree ring index increased at first, then leveled off and began to decline at about 8.5 ^{0}C for both sites. The relationships between tree ring index and minimum temperature at two year lag was different for the two sites (Fig. II.5c). For site 1, tree ring index increased with minimum temperature over the temperature range studied. Tree ring index in site 2, however, increased at first and began to decline after the temperature exceeded 8.4 ^{0}C. For both sites, the minimum temperatures at 1 and 2 year lags were more strongly

correlated with tree ring index than that of the current year (Table II.3).

Intercorrelations among climatic variables

Principal components analysis of the correlation matrix of the weather data (Table II.4) yielded three factors with eigenvalues greater than one (Table II.5). The first factor indicated that maximum summer temperatures of the current year and one year lag summer temperatures was negatively related to summer precipitation for the current year and one year lag. The second factor indicated that minimum temperature and summer precipitation were positively intercorrelated. The current year precipitation and current year maximum temperature, however, were relatively independent of their two year lags.

DISCUSSION

Most studies of tree growth in peatlands indicate that growth is limited by high water table (Boggie 1972; Boggie and Miller 1976; Jasieniuk and Johnson 1982; Mannerkoski 1985; Lieffers and Rothwell 1987b). Data from this study, however, indicated that tree growth was greatest in years with relatively high summer precipitation; these presumably are years with high water table. In natural peatlands, the vertical reach of tree roots depends more on the usual seasonal maximum than the

average water level (Mannerkoski 1985). Therefore, roots are usually restricted to positions above the usual upper limit of water table fluctuation (Boggie and Miller 1976). Black spruce in natural peatlands have shallow and spreading roots (Strong and LaRoi 1983) and roots are usually confined to hummock positions (Lieffers and Rothwell 1987b). Average productivity in peatlands is low for various reasons including the fact that tree roots occupy a small volume of substrate. In relatively wet years, water table may stay close to the surface (Munro 1984) and near these roots for most of the time; roots have good opportunities to absorb water and minerals. In dry years, the water table is much lower and trees may be under water stress; Scholander pressure bomb readings of black spruce twigs from a peatland during a hot-dry period were less than -2300 kPa (Dang, Lieffers, Rothwell and Macdonald, unpublished). It is also interesting, however, that in the two years with very high summer precipitation (>400mm) tree ring growth was reduced in the current year (Fig. II.2a) and for the next two years (Figs. II.2b and II.2c). One can speculate that heavy rainfalls in those years caused root dieback. Thus the shallow roots of these trees may be relatively ineffective at water uptake in dry years but are stressed or killed by high water levels in very wet years.

There is little information in the literature to

suggest that high air temperature limits the productivity in boreal forest ecosystems. Indeed, the reverse is usually the case (see Van Cleve et al. 1983; Mannerkoski 1985). Van Zinderen Bakker (1974), however, observed a reduction in net carbon assimilation of peatland black spruce at leaf temperature greater than 15^{0}c but all of his readings were taken at low light intensities. Nevertheless, a mean maximum temperature of 23^{o}C (Fig. II.4) should not have directly limited the tree growth in boreal forests even though many days would have had a higher maximum temperature. The fact that tree ring index decreased with increasing maximum temperature (Fig. II.4) probably relates to increased respiration rate and water stress under warm and dry conditions.

In contrast to the relationship between tree growth responses and maximum temperatures, there was generally an increase in tree growth associated with higher minimum temperatures. Low nighttime air temperatures, and presumably cool substrate, may be directly detrimental to growth because of a reduction in biochemical activity and water uptake (Running and Reid 1980; Lopushisky and Kaufmann 1984). Also, since low summer precipitations were associated with low minimum temperatures (Table II.4 and II.5), it is possible that the significant relationship between minimum temperature and growth is another expression of water stress. The most likely reason for

slow growth in years with low minimum temperatures, however, probably relates to summer frosts. Mean minimum temperatures in peatlands ranged from 3.2 to 7.4^{0}C lower than at adjacent upland weather stations and summer frosts were observed in peatlands every month in the growing season (Rothwell and Lieffers 1988). Low minimum temperatures (including frost) during summer months generally have a negative impact upon conifer growth (Van Zinderen Bakker 1974; Cannell and Smith 1984).

The lag effects of the climate on tree ring growth may have been partially caused by the autocorrelation of tree growth itself. The needles of black spruce are formed in the bud the previous year and remain on the trees for several years. The climate of a given year influences the needle formation and growth, and consequently affects photosynthesis and carbon accumulation in following years. Indeed, the preceding year's climate was the most strongly related to tree ring growth (tables II.1, II.2 and II.3). In dry land forests, the previous year's rainfall was as important to tree ring growth as current year rainfall (Tryon and True 1958; Zahner and Stage 1966).

Table II.1. Regression analysis of tree ring index (I) in relation to precipitation in the growing season (P).

Time Lag	Site 1				Site 2			
(year)	a_0	a_1	r^2	n	a_0	a_1	r^2	n
0	0.70	0.0014	0.18**	53	0.73	0.0013	0.15**	53
1	0.67	0.0015	0.23**	51	0.72	0.0013	0.17**	51
2	0.68	0.0014	0.20**	49	0.79	0.0011	0.10*	49

Note: The model is $I = a_0 + a_1 P$.

* = $p < 0.05$; ** = $p < 0.01$.

Table II.2. Regression analysis of tree ring index (I) in relation to maximum temperature (T_m) in the growing season.

Time Lag	Site 1				Site 2			
(year)	a_0	a_1	r^2	n	a_0	a_1	R^2	n
0	2.45	-0.071	0.22**	50	2.64	-0.080	0.25**	50
1	2.65	-0.081	0.29**	50	2.61	-0.077	0.25**	50
2	2.36	-0.067	0.18**	49	2.55	-0.075	0.21**	49

Note: The model is $I = a_0 + a_1 T_m$.

** = $p < 0.01$

Table II.3. Regression analysis of tree ring index (I) in relation to minimum temperature (T_n) in the growing season.

Time	Site 1					Site 2				
lag	a_0	a_1	a_2	r^2	n	a_0	a_1	a_2	r^2	n
0	0.41	0.07	-----	0.14**	50	0.67	0.04	----	0.05	50
1	-2.77	0.86	-0.049	0.30**	50	-3.45	1.07	-0.063	0.21**	50
2	-0.21	0.20	-0.007	0.25**	49	-2.54	0.84	-0.050	0.14*	49

Note: For time lag 0 the model was $I = a_0 + a_1T_n$; For time lags 1 and 2 the model was $I = a_0 + a_1T_n + a_2T_n^2$;
* = $p < 0.05$; ** $p = < 0.01$.

Table II.4 Correlation matrix of climatic variables.

	$T_m(0)$	$T_n(0)$	$T_m(1)$	$T_n(1)$	$T_m(2)$	$T_n(2)$	P(0)	P(1)	P(2)
$T_m(0)$	1.00								
$T_n(0)$	-0.07	1.00							
$T_m(1)$	0.68	-0.26	1.00						
$T_n(1)$	-0.14	0.55	-0.02	1.00					
$T_m(2)$	0.32	-0.31	0.38	-0.47	1.00				
$T_n(2)$	-0.39	0.38	-0.29	0.38	-0.12	1.00			
P(0)	-0.40	0.43	-0.27	0.39	-0.17	0.29	1.00		
P(1)	-0.33	0.26	-0.44	0.36	-0.22	0.33	0.35	1.00	
P(2)	-0.32	-0.07	-0.23	0.16	-0.42	0.39	0.00	0.23	1.00

Note: T_m = maximum temperature, T_n = minimum temperature
P = precipitation, each for the current year (0) and at one (1) and two year (2) lags.

Table II.5. Principal components analysis of climatic variables.

Variable[+]	Factor 1	Factor 2	Factor 3
$T_m(0)$	0.856	-0.020	-0.224
$T_n(0)$	-0.107	0.845	-0.014
$T_m(1)$	0.855	-0.044	-0.159
$T_n(1)$	0.056	0.829	0.360
$T_m(2)$	0.160	-0.319	-0.701
$T_n(2)$	-0.387	0.410	0.324
P(0)	-0.483	0.610	-0.193
P(1)	-0.533	0.370	0.148
P(2)	-0.221	-0.107	-0.860
Eigenvalue	3.401	1.486	1.127

[+] Indicates growing season (June to August) climatic variables

T_m = maximum temperature, T_n = minimum temperature

P = precipitation, each for the current year (0) and at one (1) and two year (2) lags.

Fig. II.1. Cross-dating among three randomly selected trees within sites and between a) site 1 and b) site 2.

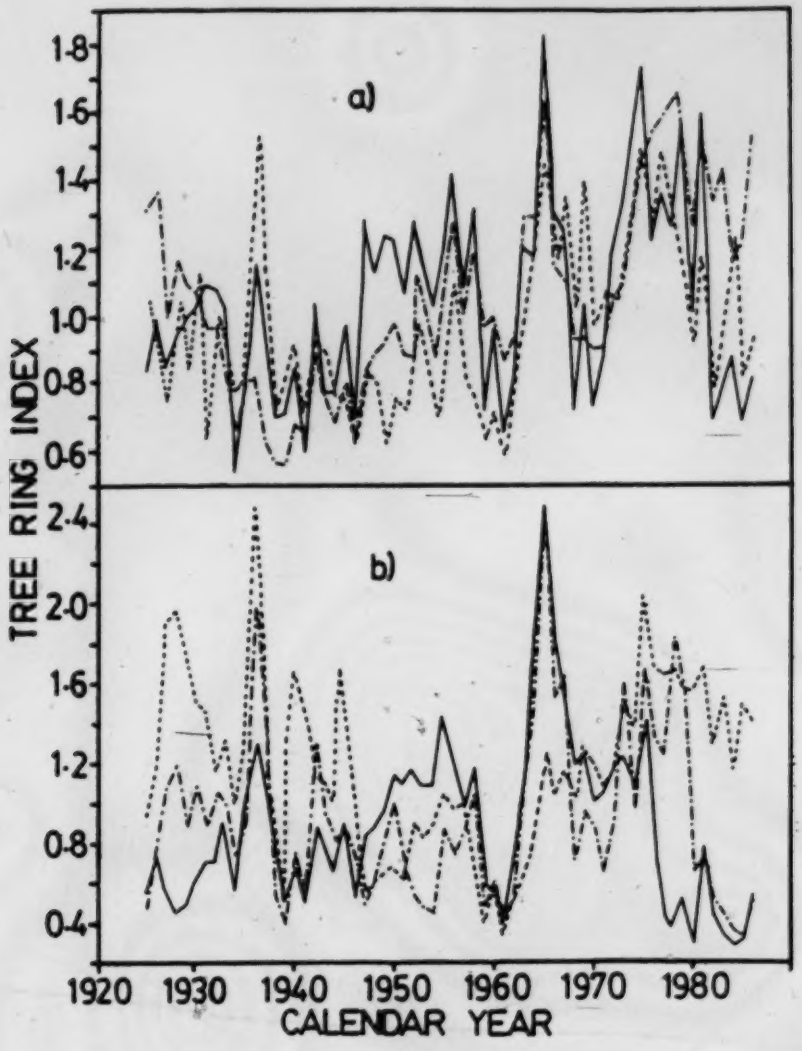


Fig. II.2. Tree ring index of black spruce in relation to June to August precipitation of a) the current year, and lags of b) one year, and c) two years for Site 1 (●; —) and site 2 (o; – – –). Note: the data points beyond 325mm precipitation were not used in the analysis.

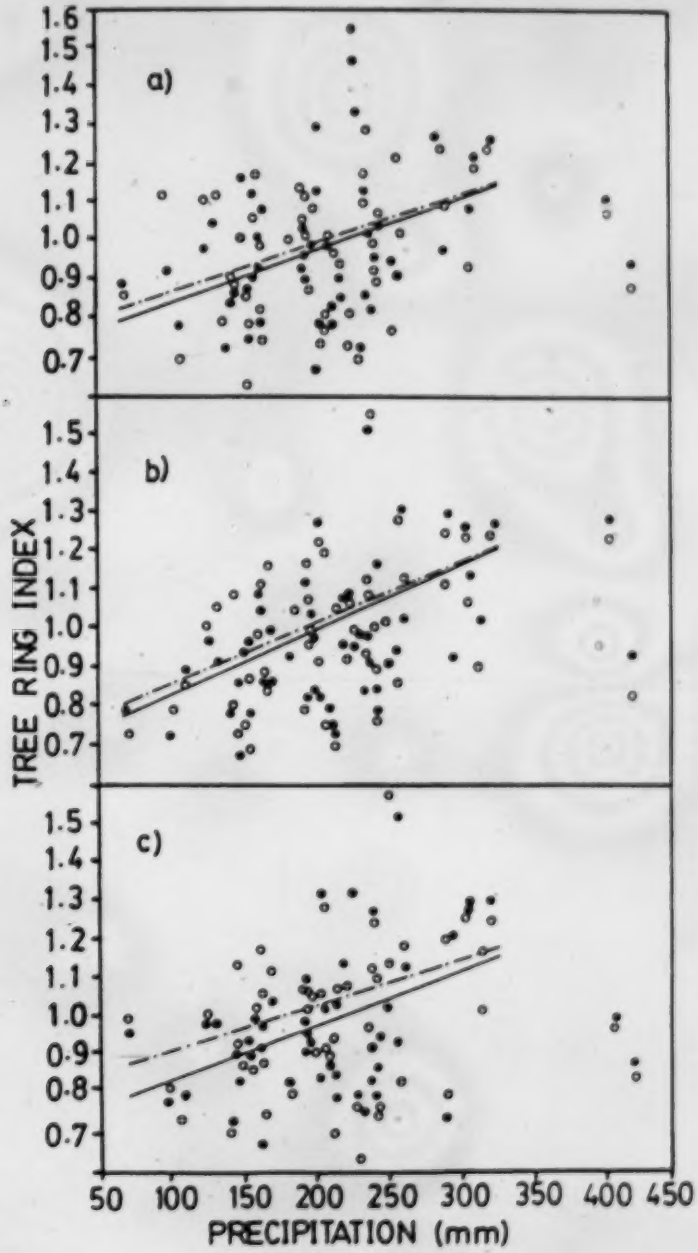


Fig. II.3. Tree ring index of black spruce in relation to mean growing season (June to August) air temperature. Site 1: ●; site 2: o.

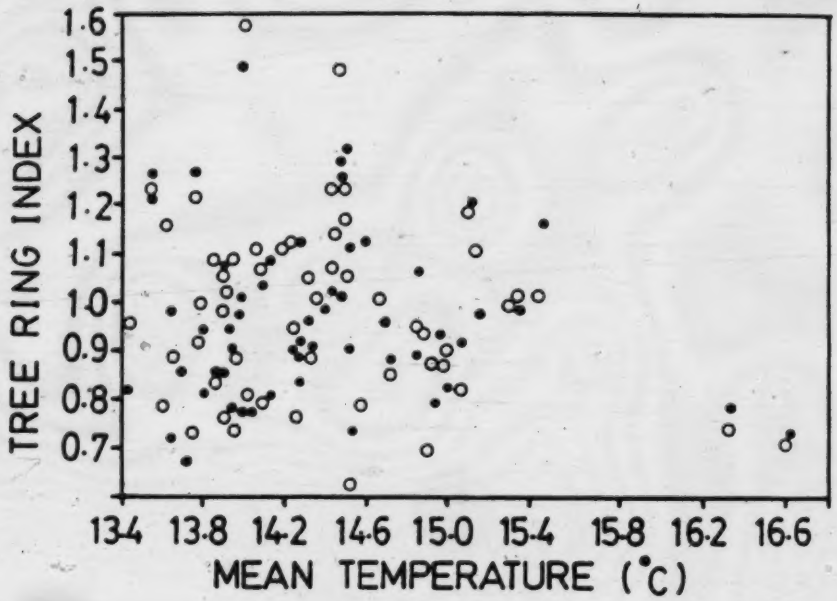


Fig. II.4. Tree ring index of black spruce in relation to maximum temperature (June to August) of a) the current year and at lags of b) one year and c) two years for Site 1 (●; ——) and site 2 (o; —·—).

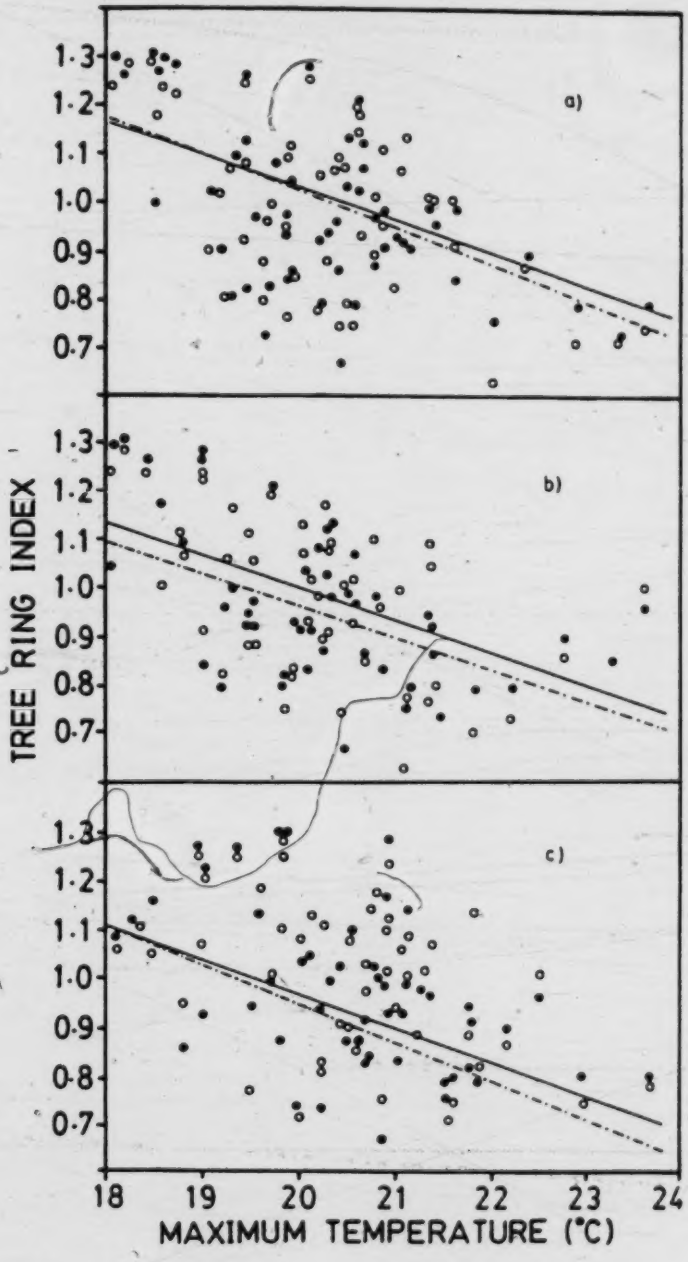
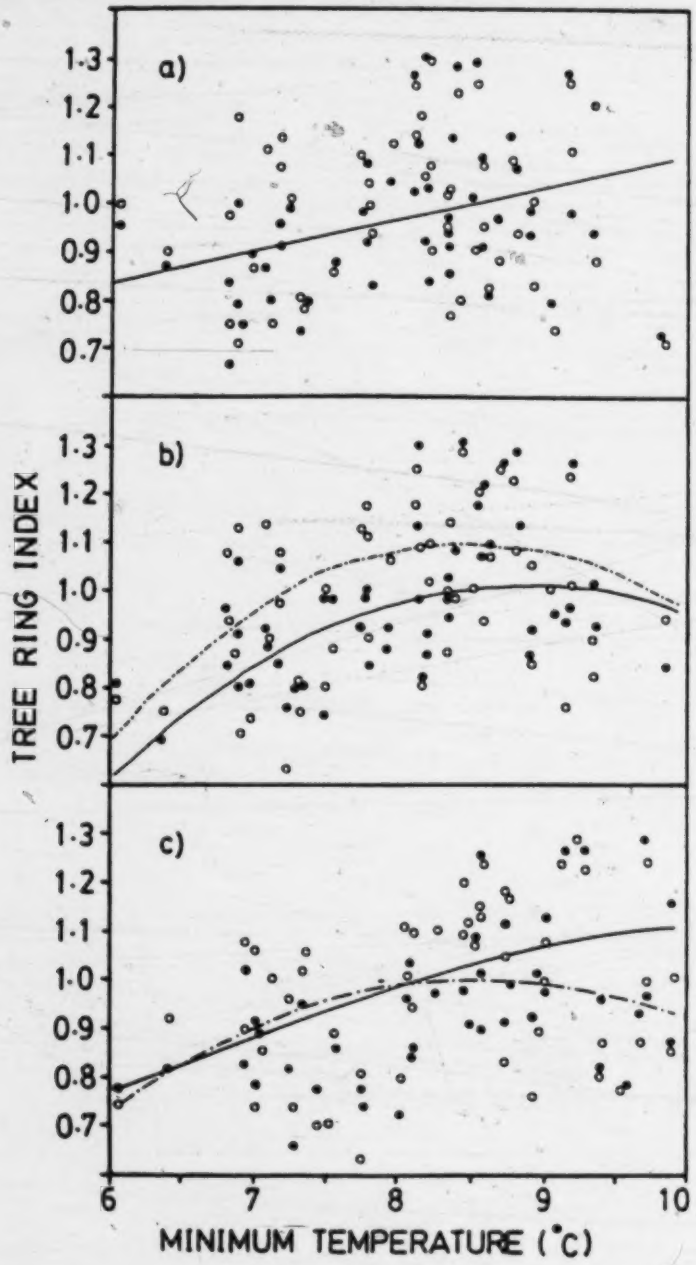


Fig. II.5. Tree ring index of black spruce in relation to minimum air temperature (June to August) of a) the current year and at lags of b) one year and c) two years for Site 1 (●,——) and site 2 (o,-·-·).



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III. ASSESSMENT AND PATTERNS OF THE RESPONSE IN ANNUAL TREE RING GROWTH OF BLACK SPRUCE FOLLOWING DRAINAGE IN SOME ALBERTA PEATLANDS

INTRODUCTION

Alberta has nearly 13 million ha of peatlands; this is about 20 percent of the total land area of the province (Tarnocai 1984; Päivänen 1985). Such vast areas of peatlands have a great potential for forestry. However, tree growth in natural peatlands is slow and productivity is generally low because of high water table, cold substrate, poor aeration, and inadequate available nutrient supply (Payandeh 1973; Lieffers and Rothwell 1987b). Trees in most Alberta peatlands rarely reach merchantable size (Lieffers and Rothwell 1986).

The tree growth in peatlands, however, can be improved by drainage. Lieffers and Rothwell (1987b) observed that the fine root biomass and the maximum rooting depth of black spruce (Picea mariana (Mill.) B.S.P.) and tamarack (Larix laricina (Du Roi) K. Koch.) increased after drainage. The improved root system in turn increases above ground growth. Large increases in diameter and height growth after drainage were reported (Heikurainen and Kuusela 1962; Stanek 1968 and 1977; Payandeh 1973; Richardson 1981; Wang et al. 1985; Trottier 1986). The total increases in tree growth, however, were not distributed evenly over the entire postdrainage period. Lieffers and Rothwell (1987a) indicated that following drainage there might be a response period when trees grow more slowly than normal. Studies from Finland (Seppälä

1969) did not report a slowing in growth but indicated that tree growth did not increase during the first few years after drainage. No quantitative studies have been conducted on the patterns of annual growth response following drainage.

Three methods have been used to evaluate the drainage effects on tree growth where drainage occurred half-way through the life of the trees. 1. Some workers (Heikurainen and Kuusela 1962; Heikurainen 1964; Stanek 1968; Payandeh 1973 and 1975; Wang et al. 1985) directly compared the average tree growth of predrainage and postdrainage. 2. Stanek (1977) estimated the drainage effects by the site index difference between the drained site and an adjacent undrained site. 3. Payandeh (1982) compared the average postdrainage tree growth of drained peatlands to adjacent undrained sites. However, there are drawbacks with these methods.

1. Generally, tree ring increment varies as the trees age, increasing at juvenile stage and later decreasing. The first method, a simple comparison of ring growth before drainage and after drainage, does not take this intrinsic trend into account. The drainage effects on tree growth estimated from this method are, therefore, inconclusive.

2. For the second method, the total height observed after drainage on a drained site is the combination of two parts: the height which was added before drainage and the

height added after drainage. Because drainage changes the site quality, the two parts follow different growth curves even though there might be a transition between them. If drainage improves site quality, then the site index of the drained site, which is determined from the postdrainage tree height, will be lower than the true site index of the current site. Thus Stanek's method underestimates the drainage effects.

3. The third method requires that the drained and control sites are in homogeneous conditions and trees in the drained and control sites are at the same age and same development stage in terms on the position in growth-age curve. In practice, however, these requirements are rarely met. In addition, none of the above three methods are capable of determining the patterns of response in tree growth following drainage. An alternative method for estimating the patterns of net response in tree growth following peatland drainage needs to be developed.

The objectives of this study were: 1. to develop a new procedure for evaluating the pattern of response of annual tree ring growth following drainage; 2. to describe the pattern of tree ring growth response of black spruce following peatland drainage.

MATERIALS AND METHODS

Study sites and data collection

The study area is located east of Slave Lake, Alberta, along the provincial highway #2. The highway was built in 1966, across a treed fen (Lieffers and Rothwell 1987b). The road bed and associated ditches interrupt local shallow ground water flow, resulting in lower water table downslope. Upslope of the road, water levels near the ditch were also lowered, but on the same side and farther away from the ditch the water table was not influenced by the road building. This situation provided a natural drainage experiment for this study. Stanek (1977), Payandeh (1982), Wang et al. (1985), and Lieffers and Rothwell (1987b) used similar situations to study the effects of drainage on tree growth.

The forests in this area are dominated by black spruce (Picea mariana (Mill.) B.S.P.) with scattered tamarack (Larix laricina (Du Roi) K. Koch.). Understory is dominated by Ledum groenlandicum Oeder, Rubus chamaemorus L., Sphagnum magellanicum Brid and S. warnstorfii Russ. On the drained site, Pleurozium schreberi (Brid.) Mitt and Hylocomium splendens. (Hedw.) B.S.G. are more abundant.

Six drained peatland sites were selected. They were located at $55^0$10′N $114^0$16′30"W, $55^0$10′45"N $114^0$20′W, $55^0$10′15"N $114^0$17′W, $55^0$11′N $114^0$20′30"W, $55^0$09′25" $114^0$13′30"W, and $55^0$07′25"N $114^0$10′10"W respectively.

Black spruce trees on these ranged from 54 to 128 years old. Downslope of the highway, plots were laid out at 5m from the road right-of-way. Plots upslope of the road, 70 to 100m from the cleared right-of-way, were chosen as control sites. Each site (both drained and undrained) had two replicate plots which were 10m apart and parallel to the highway. All the sites (both drained and undrained) were distributed in similar landforms and appeared to have similar species composition. The trees in the drained sites had about the same average age as those in the corresponding undrained sites. The uniformity of those sites prior to the road construction were confirmed by examining 1965 aerial photographs of this area.

In June 1987, a 5cm diameter perforated plastic pipe was installed in the centre of each of the plots (both drained and undrained). The depth to water table in the pipes was measured biweekly from June 11 to August 26, 1987. In mid-September of the same year, ten dominant-codominant black spruce were selected from each plot (both drained and undrained sites). Cross-sections at the tree base and 30cm height position were cut from each tree for age and tree ring increment measurement respectively. Tree heights were also recorded for calculating site index. The discs were air dried and sanded by a belt sander. The annual tree ring increments at four radii along the longest and the shortest diameters of each disc were

measured on a computerized measuring device (Clyde and Titus 1987). Cross-dating was conducted among trees and among sites (see methods in chapter 2).

Analysis

Estimation of tree ring index for drained sites

As shown by comparing the general forms of tree ring increment from the undrained site (Fig. III.1) and drained site (Fig. III.2), the ring growth in the drained site increased following drainage. In order to estimate this change, one first needs to estimate the usual curve of tree ring growth in the drained site for the postdrainage period, which the tree growth would follow if the peatland were not drained. The procedures are as follows: A negative exponential function was fit by regression procedures to the observed tree ring increment data from the drained site for the period from the growth peak to the time of drainage (Fig. III.3). All the regression coefficients were significant at 0.05 level and most at 0.01 level (Table III.1) and only a small number of equations had a problem with non-normality of residuals (Table III.2). Each observed tree ring increment, both predrainage and post drainage, was then divided by the corresponding growth value obtained from the regression equation, to give the tree ring index (Fritts 1976).

Test for the validity of extrapolation

The test for validity of this technique is as

follows: Negative exponential functions were also applied to the tree ring data from the undrained site, firstly for the period from the growth peak to the time of drainage and secondly from the growth peak to the time of sampling. Thus two equations were generated for the same tree. By dividing each observed tree ring increment by the predicted values from the above two different equations, two sets of tree ring indices were obtained for each tree. The first equation and the tree ring indices derived from it, however, estimated the postdrainage tree ring growth by extrapolation of the equation similar to the procedures for the drained site. Paired t-test (Table III.3) showed that for the postdrainage period the mean of the differences between pairs of tree ring indices were not significantly different from zero at 0.05 level for most of the trees and at 0.01 level for all of the trees. Where significant, t values were positive for some trees but negative for others, suggesting the technique was unbiased. This indicated that the extrapolation technique was reasonably good for predicting the postdrainage tree ring increments for the drained site.

Estimation of tree ring response to drainage

Difference in the means of tree ring indices between drained and corresponding undrained sites for the postdrainage period was examined by analysis of variance. The tree ring indices for all of the trees at the same site

were then averaged (separately for drained and undrained sites) year by year, getting the average tree ring index series for each site. Tree ring indices of the drained site generally had a similar pattern of fluctuation for both predrainage and postdrainage periods, suggesting the tree ring growth of the drained and undrained sites responded similarly to environmental fluctuations for both predrainage and postdrainage periods. The average tree ring index series of the undrained site was, therefore, subtracted from that of the corresponding drained site year by year and differences for the postdrainage period were used as estimators of net response of tree ring growth to drainage. The net response values were plotted against the time elapsed (in years) after drainage.

Variables for growth response and site quality

The period immediately following drainage, in which the net responses were around zero, was defined as the initial response period. The average slope from the point of minimum net response to that of the maximum net response was defined as increase rate. The length of the initial response period, increase rate, maximum net responses and the time from the year of draining to the year of maximum net response were compared to the tree age and site index at the time of drainage and the difference in average postdrainage water table between the drained site and corresponding undrained site. The initial site index was

estimated by the site index of the undrained site and calculated by the following formula (Alberta For. Serv. 1985):

$$SI = 9.9531 + 0.4751*HT - 0.6659*\ln^2(STAGE) + 6.0486*HT/STAGE - 0.00285*STAGE*\ln(STAGE)$$

Where: SI = Site index, total height at 50 years at breast height; HT = Average height of dominant-codominant trees weighted by basal area; STAGE = Age at the tree base; ln = Natural logarithm.

RESULTS

The tree ring indices of the drained and undrained sites generally had similar patterns of year to year fluctuations for both predrainage and postdrainage periods (Fig. III.4). This suggests that the drained and undrained sites generally had similar relationships with environmental fluctuations for the postdrainage period as well as the predrainage period. However, the average tree ring indices from all of the drained sites were significantly greater than those of the corresponding undrained sites for the postdrainage period (Table III.4). But the net increases were not distributed evenly over the 21 years after drainage (Fig. III.5). In the first few years after drainage, the average difference in tree ring index between drained site and undrained site was below zero for some of the sites but above zero for others (Fig. III.5). However, compared with the values in the

predrainage period, the deviations from zero in this period were generally small. This indicated that in the initial response period the tree ring growth was not affected by drainage. The length of initial response period varied from 3 to 6 years (Fig. III.4). After this period, however, the net increase values increased linearly with time (Fig. III.5). The increase rates varied from 6% to 69% per year. The net increase reached maximum between 13 to 19 years after drainage. The maximum values of net increases ranged from 76% to 766%. The net relative increases fluctuated at values near the maximum there after.

The data also appeared to indicate that the amount of water table drop after drainage had a positive impact on the response of tree ring growth to drainage, but the initial tree age and site index had negative effects (Table III.5). However, there were not sufficient data for any conclusions to be drawn regarding these aspects in the current study.

DISCUSSION

Methodology for Estimation of Postdrainage Response

The negative exponential function is an important component in most of the commonly used models describing tree ring or diameter increment (Fritts 1976). It adequately describes the trend of tree ring growth after

the growth peak in the juvenile phase. This is, however, the first time that the net effects of peatland drainage on the tree ring growth were estimated using dendrochronological techniques. These methods allow the determination of the net response of tree growth to peatland drainage on a yearly basis, which is generally free of intrinsic trend of tree growth and macroenvironmental effects. These methods can also be used in other situations where net treatment effects on tree ring growth are desired (e.g. estimating air pollution effects on tree growth).

The methods used in this paper use both the tree ring growth in a control site and the predrainage growth of the drained site as controls for postdrainage tree growth of the drained site. They have no strict requirements on site quality or tree age on control sites. They only require that the drained and control sites are in the same general area. The output from these methods is net relative increase and comparable between different regions and sites with different initial site quality and/or different tree ages. These methods, therefore, logically should be more accurate and practical than traditional procedures. The precision of these methods, however, depends on the length of the period the tree ring increments of which are used for developing the regression equation. If this period is too short, the regression line

could deviate considerably from the true growth trend and result in unreliable predictions for postdrainage tree growth.

Comparison of the technique developed in this thesis for assessing peatland drainage effect on tree growth with techniques used in watershed and fertilization experiments

1. Objectives are similar.

a. In watershed experiment, it is to test whether log-harvesting increases water flow.

b. In fertilization experiment, it is to test whether fertilizers increase tree growth.

c. In this thesis, the objective is to examine the pattern of tree ring growth response to peatland drainage.

2. Summary of techniques.

a. The procedures for estimating the effect of log-harvesting on daily water flow consist of four steps (Goodell 1951 and 1958; also see Fig. III.6):

I. Take ratio of the daily water flow from whatershed A (log-harvested) to that from watershed B (control) for pretreatment period:

$$R_w = T_{w1} / C_{w1}$$

II. Model the relationship between R_w and the number of days (t) from spring rise:

$$R_w(t) = a + b*t$$

III. Predict the posttreatment water flow

of watershed A from the corresponding value of watershed B (C_{w2}) and $R_w(t)$:

$$T_{wp} = C_{w2} * R_w(t)$$

IV. Calculate treatment effect:

$$E_w = T_{w2} - T_{wp}$$

where T_{w2} = observed posttreatment water flow from watershed A.

b. The procedures for estimating fertilization effect on tree growth consist of three steps (Salonius et al. 1982; Ballard and Majid 1985; also see Fig. III.7).

I. Take ratio of posttreatment periodic growth to pretreatment growth for the control site:

$$R_F = C_{F2} / C_{F1}$$

II. Predict posttreatment periodic growth of the fertilized site from its own pretreatment growth (T_{F1}) and R_F:

$$T_{Fp} = T_{F1} * R_F$$

III. Calculate fertilization effect:

$$E_F = T_{F2} - T_{Fp}$$

where T_{F2} = observed posttreatment growth of the fertilized site.

c. The procedures for estimating drainage effect on tree ring growth consist of five steps (see Fig. III.7):

I. Fit growth curve T_D for the predrainage tree ring increments of the drained site and extrapolate it for the postdrainage period.

II. Calculate tree ring index for the drained site:

$$I_D = \text{observed} / T_D$$

III. Fit growth curve C_D to the tree ring increments of the control site for the whole period.

IV. Calculate tree ring index for the control site:

$$I_C = \text{observed} / C_D$$

V. Estimate net yearly effect of drainage:

$$E = I_D - I_C$$

3. Important similarities and differences

The above three techniques are similar in that they all use both pretreatment tree-growth/water-flow of treated site and of control site to assess treatment effects. The technique for estimating log-harvesting effect on water flow and that for estimating drainage effect on tree ring growth are identical in that both of them can produce a response pattern. However, the above three techniques apply to different situations and work under different assumptions.

The technique for watershed experiment applies to cyclic events, where the relationship between R_w and t can be determined in one or more cycles. In addition, the response of water flow to log-harvesting is immediate, which is in contrast to the graduate response of tree growth to fertilization/drainage.

The technique for fertilization studies works under the assumptions that trees in the experimental and control sites must have the same age and the growth curves for the two sites must be parallel to each other. If the assumptions are not met, results from this method can be misleading. In practice, however, the second assumption is rarely met. In addition, this method can not estimate response pattern.

In contrast, the technique developed in this thesis can be applied to any situations where the total, average and/or response patterns are desired. It has no assumptions on the tree age or paralleling of growth curves which are required by the method in fertilization. According to definition (Fritts 1976), tree ring indices have a mean of 1 if there is no treatment effect. Therefore, the tree ring indices themselves are good estimates of treatment effect if there are no other factors affecting the tree ring growth trend. This means that in some situations this method can give reasonably good estimates of treatment effects without using control site. However, the function of control site in this method is to eliminate the effects of other factors (including climatic fluctuations) on tree growth, to give estimation of net response. Therefore, control sites are recommended whenever possible.

Tree Growth after Drainage

While the relationship between climate and tree ring growth of black spruce on natural peatlands has been studied (See chapter 2), there is little information on the relationship between climate and tree ring growth of black spruce on drained peatlands. In natural peatlands, tree ring growth of black spruce is positively related to summer precipitation and minimum temperature, but negatively related to summer maximum temperature (See results in chapter 2). From the reasonably good cross-dating of tree ring indices between drained and undrained peatlands (Fig. III.4), it appears that the above relationships between tree growth and climate may still hold for black spruce in drained peatlands. This indicates that black spruce, both on drained and undrained peatlands, probably experiences similar environmental stresses.

Even though the drainage improves substrate aeration and speeds decomposition of organic matter (Lahde 1966 cited by Mannerkoski (1985)), the change in growth rates in response to these improved conditions is not immediate. The root system (Lieffers and Rothwell 1987b) and leaf area of black spruce in natural peatlands is small. In early stages after drainage the amount of photosynthetic products necessary for extending the root system and leaf area is probably also low. Therefore immediately following drainage, no or little increase in tree ring growth is

possible as the trees are probably allocating resources to develop root systems and leaf area. Indeed, the net change of tree ring index during the first 3 to 6 years after drainage was around zero for all the sites in this study (Fig. III.5). This result is in good agreement with Finnish studies (Seppälä 1969). The 13 to 19 years for the trees to reach a stable condition after drainage probably relates to the same factors of gradual development of roots and leaf area. It may also relate to the gradual increase in available nutrients and improvement in substrate conditions. It is difficult to isolate the sources of the increased tree ring growth. The improvement in tree root systems, leaf area and substrate conditions are themselves interrelated.

Table III.1 Test for significance of regression equations for the drained site using data from the time of peak growth to the time of drainage.

Tree	r	n	Tree	r	n	Tree	r	n
1.1-2+	-0.456*	19	1.2-3	-0.647**	18	1.2-2	-0.739**	19
1.2-5	-0.902**	22	1.2-9	-0.942**	21	2.1-5	-0.674**	30
2.1-6	-0.683**	22	2.2-4	-0.692**	20	2.2-7	-0.600**	21
2.2-8	-0.512*	21	3.1-4	-0.818**	15	3.1-7	-0.719**	20
3.1-9	-0.725**	20	3.2-3	-0.905**	23	3.2-7	-0.751**	22
4.1-6	-0.536*	19	4.1-7	-0.512*	20	4.1-8	-0.718**	22
4.2-6	-0.612**	20	4.2-8	-0.615**	19	5.1-1	-0.836**	52
5.1-2	-0.722**	31	5.2-1	-0.627**	60	5.2-7	-0.623**	31
5.2-9	-0.627**	40	6.1-2	-0.437**	26	6.1-5	-0.796**	60
6.2-1	-0.437**	43	6.2-4	-0.653**	65	6.2-5	-0.452*	26

Note: r = correlation coefficient; n = number of data points used in developing the regression equation;
* = $P < 0.05$; ** = $P < 0.01$.

+ The three numbers are site, replicate number within site, and tree number within site, respectively. The trees listed in this table were selected randomly from all the samples, five tree from each site.

Table III.2 Test for the normality of regression residuals from equations from the drained site, using data from the time of peak growth to the time of drainage.

Tree No.	X^2	Tree No.	X^2	Tree No.	X^2
1.1-2+	4.295 ns	1.2-3	0.769 ns	1.2-2	2.773 ns
1.2-5	3.347 ns	1.2-9	1.596 ns	2.1-5	6.528 ns
2.1-6	8.095 *	2.2-4	2.001 ns	2.2-8	1.451 ns
2.2-8	2.072 ns	3.1-4	1.144 ns	3.1-7	2.784 ns
3.1-9	10.682 *	3.2-3	6.174 ns	3.2-7	3.489 ns
4.1-6	3.301 ns	4.1-8	8.637 *	4.1-7	1.334 ns
4.2-6	3.379 ns	4.2-8	1.079 ns	5.1-1	4.483 ns
5.1-2	4.383 ns	5.2-1	2.810 ns	5.2-7	5.877 ns
5.2-9	2.810 ns	6.1-2	1.534 ns	6.1-5	6.024 ns
6.2-1	2.209 ns	6.2-4	2.227 ns	6.2-5	5.646 ns

Note: X^2 = "Chi Square" test statistic; ns = not significant at 0.05 level; * = $p < 0.05$; the degree of freedom is 3 for all the X^2 tests.

+ See Table 1 for explanation of tree codes.

Table III.3. Paired t-test for differences between postdrainage tree ring indices from undrained sites obtained by different methods (see methods).

Tree No.	t value	Tree NO.	t value	Tree No.	t value
1.1-2+	-1.21 ns	1.1-3	0.76 ns	1.2-2	1.27 ns
1.2-5	-1.39 ns	1.2-9	-2.17 *	2.1-5	-1.14 ns
2.1-6	0.12 ns	2.2-4	-0.39 ns	2.2-7	0.14 ns
2.2-8	-1.63 ns	3.1-4	-1.55 ns	3.1-7	-1.14 ns
3.1-9	-0.23 ns	3.2-3	-1.32 ns	3.2-7	-1.27 ns
4.1-6	-1.40 ns	4.1-8	0.33 ns	4.1-9	-0.25 ns
4.2-6	-0.84 ns	4.2-8	1.90 ns	5.1-1	-1.39 ns
5.1-2	-1.69 ns	5.2-1	0.81 ns	5.2-7	0.30 ns
5.2-9	0.81 ns	6.1-2	-0.10 ns	6.1-5	-0.18 ns
6.2-1	-2.12 *	6.2-4	-1.53 ns	6.2-5	2.62 *

Note: The degree of freedom for all the tests is 20;
ns = not significant at 0.05 level; * = $p < 0.05$

+ See Table 1 for explanation of tree codes.

Table III.4. Analysis of variance for difference in the means of postdrainage tree ring indices between drained and undrained sites.

Site No.	SS.t.	df.t.	SS.e	df.e	F ratio
1	132.67	1	14.90	34	8.90 **
2	32.58	1	0.81	35	40.22 **
3	36.44	1	1.92	32	19.02 **
4	9.23	1	2.07	36	4.46 *
5	0.89	1	0.20	33	4.45 *
6	32.58	1	0.94	34	34.76 **

Note: SS.t. and df.t. are sum of squares and degree of freedom respectively for treatment; SS.e. and df.e. are the sum of squares and degree of freedom respectively for the error term; * = $P < 0.05$; ** = $P < 0.01$.

Table III.5 Postdrainage changes in tree ring index in relation to the tree age and site index at the time of drainage, and depth to water table* after drainage.

No.	AGE	DRAINED DEPTH (cm)	CONTROL DEPTH (cm)	DEPTH+ DIFF. (cm)	S.I.	IP	IA	IR	MAX	YM
1	33	87.9+	30.9+	57.0	8.0	4	4.70	0.69	7.66	17
2	41	61.5	42.8	18.7	7.0	6	2.02	0.27	4.80	18
3	43	87.0	53.4	33.6	8.5	5	2.01	0.31	4.93	18
4	45	45.0	27.6	17.4	8.2	5	1.01	0.16	2.86	19
5	49	59.1	38.2	20.9	9.1	6	0.46	0.06	0.76	13
6	107	69.0	45.1	23.9	2.8	3	0.97	0.13	2.82	19

* The values of depth to water table are the averages of seven measurements taken on June 11, 23, July 7, 20 and August 4, 13 and 26, 1987.

+ DEPTH DIFF. = DRAINED DEPTH - CONTROL DEPTH.

Note: AGE = tree age at the time of draining; S.I. = initial site index (tree height in meters at the age of 50) calculated from the tree height and age of the undrained site; IP = the length of initial response period; IA = average of the changes in tree ring index after drainage; IR = increase of tree ring index per year in the postdrainage period; MAX = maximum increase of tree ring index after drainage; YM = years from the time of drainage to the time of maximum increase.

Fig. III.1 Tree ring increment at 30cm height of a black spruce from an undrained peatland. Age was determined at 30cm height.

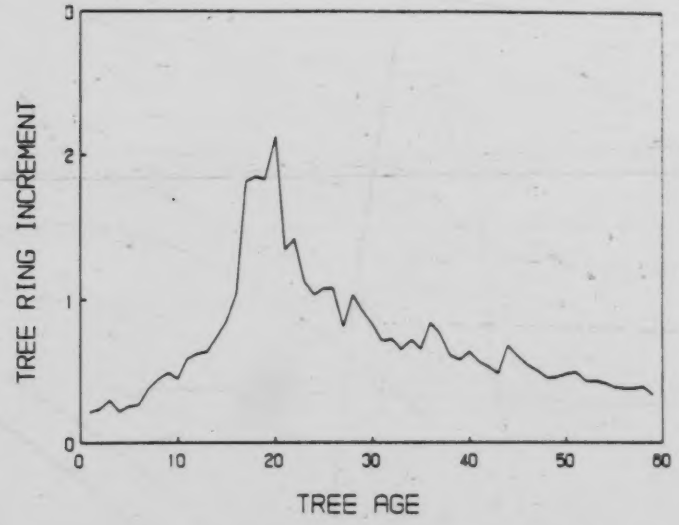


Fig. III.2 Tree ring increment at 30cm height of black spruce from a drained peatland. Arrow indicates the time of draining. Age was determined at 30cm height.

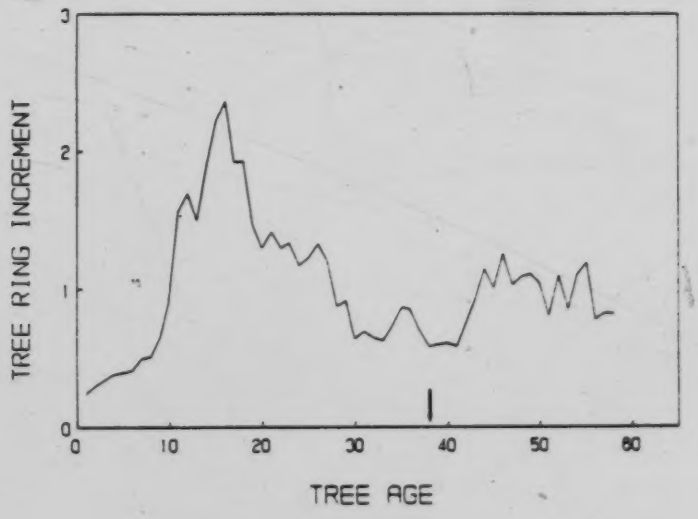


Fig. III.3 Tree ring increment of the same tree as in Fig. III.2 with trend line (—·—) for the period from peak growth to drainage and its extrapolation (·····) into the postdrainage period. The equation of the trend line is: $\ln(I) = 1.5019 - 0.0539 * AGE$, where I = tree ring increment, AGE = tree age, $r^2=0.839$, n=23.

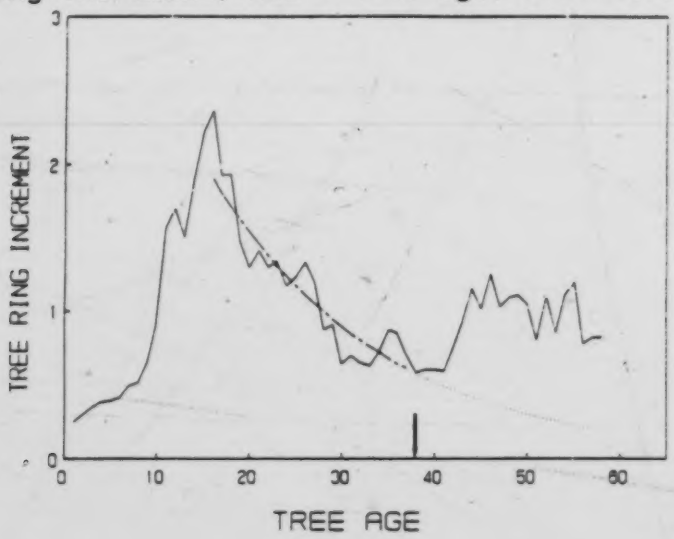


Fig. III.4 Tree ring indices of black spruce from Site 1 (——) and its control site (—·—) for both predrainage and postdrainage periods.

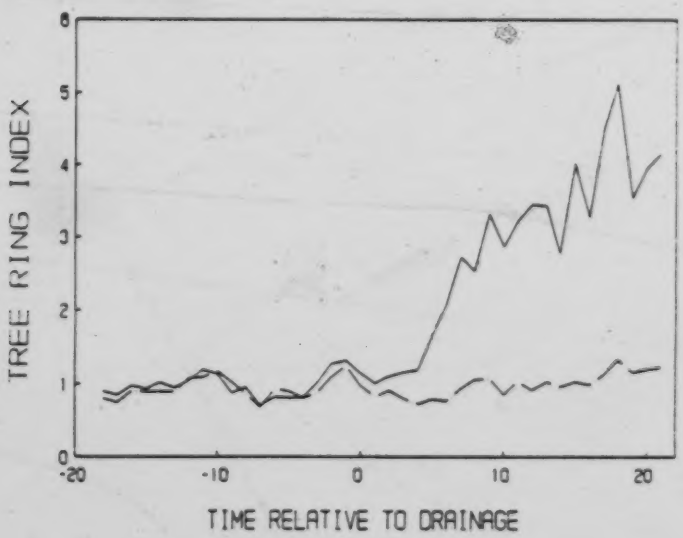


Fig. III.5 Differences in tree ring indices of black spruce between drained and undrained sites before and after drainage from six Alberta peatlands. The time of drainage is indicated by a time value of 0; the tree ages at the time of draining are 33, 41, 43, 45, 49 and 107 for the six sites listed sequentially from top to bottom.

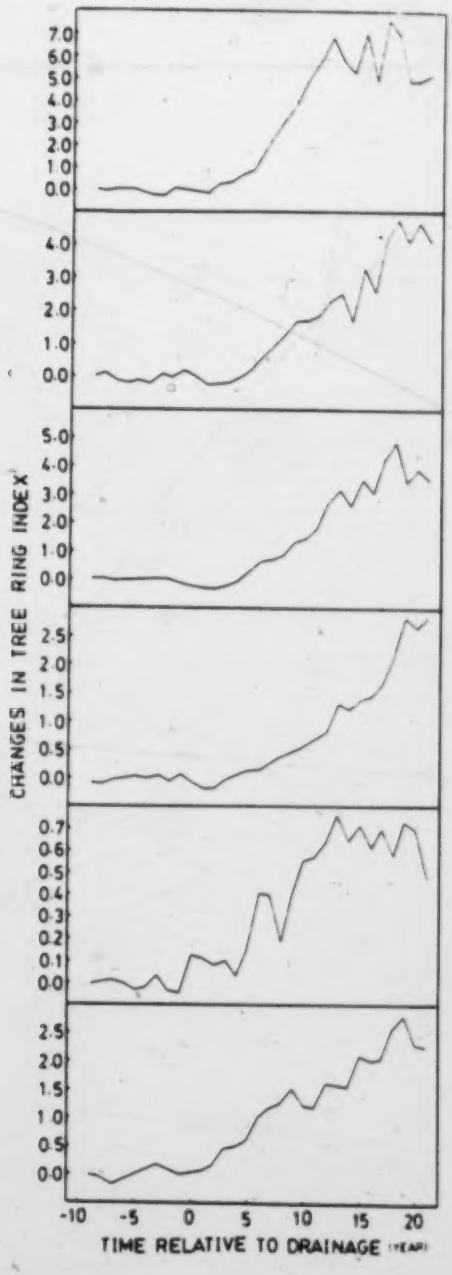


Fig. III.6 Water flow from log-harvested (T_w) and control (C_w) watersheds. The subscripts 1, 2 and p indicates pretreatment, posttreatment, and predicted posttreatment water flow respectively. The vertical line indicates the time of log harvesting.

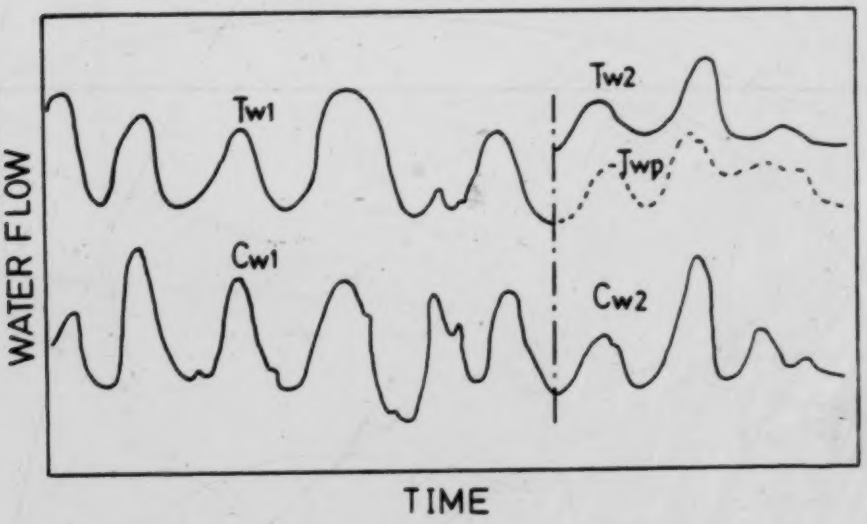
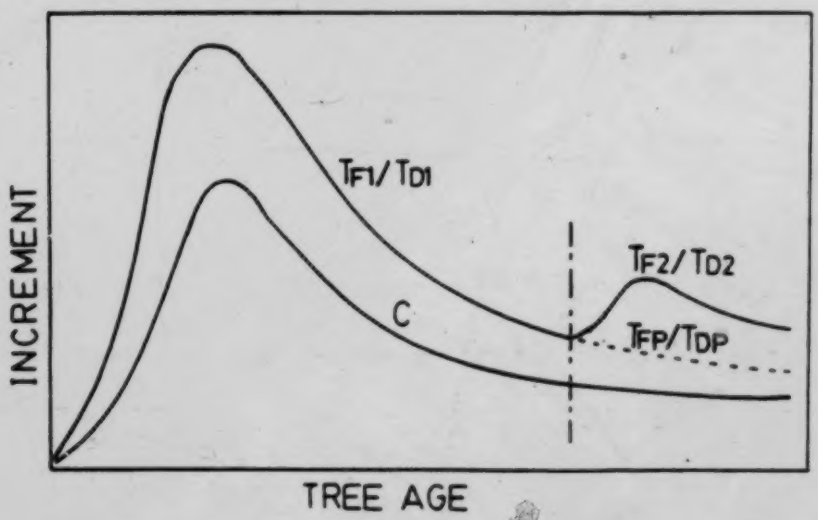


Fig. III.7 Tree ring increment of fertilized/drained (T_F/T_D) and control (C) sites. The subscripts 1, 2 and p indicates pretreatment, posttreatment and predicted respectively. The vertical line indicates the time of treatment.



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GENERAL DISCUSSION

Water relations are generally one of the most important factors in the relationship between climate and tree ring growth (Fritts 1976; Kramer et al. 1979). Even though peatlands are generally considered to have an excess amount of water, the data suggest that black spruce is probably under water stress in years with low summer precipitation and high daytime temperature. Black spruce typically has a shallow root system (Strong and LaRoi 1983) and the root resistance to water is high (Van Zinderen Bakker 1974). In years with low precipitation and high daytime temperature, the shallow root system may not be able to replenish the increased water loss caused by high transpiration rates under warm conditions. This may result in stomata closure and decreased carbon assimilation. In addition, under warm conditions, respiration at high rates consumes more carbohydrates. Therefore, trees attain less growth in dry years with higher daytime temperature than in relatively wet and cool years. However, if the summer precipitation is too high, the whole root systems will be flooded and probably die back. Roots might lose their ability to absorb water after a period of flooding while transpiration from the needles might be still continuing. This might also cause severe water stress and even needle cast, resulting in decreases in tree growth for the current year and following years.

Low precipitation and high daytime temperature are

accompanied by low nighttime temperature (Table II.5). Low minimum air temperature and presumably cool substrate are detrimental to tree growth (Running and Reid 1980; Lopushisky and Kaufmann 1984). But more importantly, low nighttime are generally associated with summer frosts, which severely inhibits net carbon assimilation (Van Zinderen Bakker 1974).

Drainage improves substrate conditions and increases size of root systems (Lieffers and Rothwell 1987). Concomitantly, the daily temperature fluctuation range also increases after drainage, i.e. after drainage daily maximum temperatures increase but minimum temperatures decrease (Pessi 1958). Thus in drained peatlands, tree growth might be also limited by water stress and summer frost in dry years with high maximum temperature and low minimum temperature.

In the study of tree ring growth on natural peatlands, relative high growing season precipitation and presumably a high water table produced the best tree growth. In contrast, previous studies as well as information from chapter 3 have shown that drainage increases tree growth. These seemingly contradictory results can probably be explained as follows: During the course of natural water table fluctuation in natural peatlands, the water table drop is temporary and does not result in sustained improvement in the substrate conditions

(Mannerkoski 1985) or root system. Generally, a direct consequence of the water table drop and associated high daytime temperature is probably water stress to trees. In contrast, the permanent lowering in water table after drainage can considerably improve the aeration and nutrient status in the substrate (Lahde 1966 cited by Mannerkoski (1985)), and provide favorable conditions for tree root growth. However, the rate of change is generally slow. It takes the trees 3 to 6 years for the trees to react to drainage and 13 to 19 year to reach a stable growing condition.

The experiment on peatland drainage in this study was uncontrolled, the results are therefore preliminary. The techniques developed in this study for evaluating drainage effects on tree ring growth, however, can be applied to various studies where treatment effects on tree growth need to be assessed.

The work and investigation in this thesis stimulated other research questions related to the tree growth in drained and natural peatlands:

1) What are the patterns of water relations, stomatal aperture, photosynthesis rates, and leaf temperature?

2) How are the water relations, stomatal behaviour and photosynthetic output of peatland trees affected by temperature, light, ambient and soil moisture conditions?

3) What is the relationship between photosynthesis

rate and water relations?

4) Under what ambient and soil conditions are peatland trees under water stress?

5) Do the leaf stomata respond in a similar way to environmental fluctuations in drained and natural peatlands?

6) Are there any major changes in tree physiology after peatland drainage which make the trees in drained site grow faster?

7) What are the best predictors for postdrainage performance of peatland trees?

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